J Raptor Res. 26(2):74-80

SOCIAL HUNTING IN BROODS OF TWO AND FIVE AMERICAN KESTRELS AFTER FLEDGING

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Abstract.—Young American Kestrels (*Falco sparverius*) presumably learn hunting skills during the first 4–6 wk after fledging. Imitative social hunting during this period may provide an adaptive advantage later in the juvenile period, if there is sufficient selection for learned efficiency in hunting. We report the results of a test of the hypothesis that imitative hunting in large broods increases hunting efficiency of American Kestrels after fledging. We experimentally adjusted the size of kestrel broods prior to fledging to two or five young. No differences in hunting efficiency were detected during the 4 wk of observation. Sample sizes, however, were small because of high mortality or signal failure among radio-marked birds. Most deaths occurred during the first week after fledging, and predation was the main cause of mortality.

Cacería en sociedad de dos a cinco crías de Halcón Cernícalo (*Falco sparverius*), después de haber dejado el nido

Extracto.—Se supone que el Halcon Cernícalo (*Falco sparverius*) joven, aprende la destreza en la cacería durante las primeras 4–6 semanas después de haber dejado el nido. La imitación, implícita en cacerías sociales, puede proveer una ventaja en la adaptación posterior del período juvenil, si es que hay suficiente selección de eficiencia aprendida. Informamos los resultados de una prueba sobre la hipótesis de que la caza imitativa, en jóvenes de nidadas grandes, aumenta la eficiencia en cazar del Halón Cernícalo después de haber dejado el nido. Experimentalmente, a la nidada de estos halcones, la hemos ajustado a un tamaño entre dos y cinco crías antes de que hayan salido del nido. No se detectaron diferencias en la eficiencia en cazar durante las 4 semanas de observación. Los tamaños de las muestras, sin embargo, fueron pequeñas debido a la alta mortalidad, o a la falla del equipo en las aves marcadas con radiotransmisores. La mayoría de las muertes acurrió durante la primera semana después de haber dejado el nido. La predación fue una causa principal de la mortalidad.

[Traducción de Eudoxio Paredes-Ruiz]

Wilson (1975:51) described two types of social hunting, imitative and cooperative. During imitative hunting individuals observe others and may initiate, copy, increase, or learn hunting behavior. According to Wilson, "the animal simply goes where the group goes, and eats what it eats." Cooperative hunters usually use a signal (or signals) to coordinate pursuit, whereas during imitative hunting, communication is thought to be without signals and group members do not divide labor (Hector 1986). Several investigators have reported feeding benefits associated with imitative hunting (e.g., Krebs 1973, Rubenstein et al. 1977, Sullivan 1984, Edwards 1989a, 1989b). Edwards (1989a, 1989b) compared the hunting behavior of sibling pairs of Ospreys (*Pandion haliaetus*) and singletons, and found that pairs developed hunting skills sooner, used similar hunting techniques, and had similar diets.

Hector (1986) reported that imitative hunting (as defined by Wilson) is more common than cooperative hunting among raptors, and he cited several examples of species that hunt in this manner. Kellner (1990) observed imitative hunting in one sibling group of five kestrels, and among three of these siblings and five other juveniles. Other anecdotal accounts of imitative hunting include observations of up to 20 juveniles hunting in a single field (Cade 1955), 18 juveniles "perched along one short stretch of road" (Wheeler 1979), and aggregations of as many as 14 juveniles and adults on reclaimed surface mines (Wilmers 1982).

In 1988 we began a study of the post-fledging

Table 1. Percent time (mean percent ± SE) engaged in 10 behaviors by broods of two and five American Kestrels at weekly intervals after fledging in Iowa.

		WEEKS POST-FLEDGING				1–4 P-VALUES[a]		
		1	2	3	4			TIME ×
BEHAVIOR	BROOD SIZE	MEAN ± SE	MEAN ± SE	MEAN ± SE	MEAN ± SE	BROOD SIZE	TIME	BROOD SIZE
(N)[b]	2	(8)	(5)	(5)	(3)			
	5	(8)	(8)	(7)	(7)			
Perch resting	2	77.4 ± 6.1	63.5 ± 7.7	34.2 ± 9.7	21.0 ± 10.0	0.473	<0.001	0.156
	5	78.2 ± 4.6	69.4 ± 3.5	46.3 ± 4.2	39.0 ± 9.2			
Perch hunting	2	0.0	5.6 ± 5.6	42.4 ± 15.9	56.4 ± 11.0	0.263	<0.001	0.231
	5	0.0	4.2 ± 3.0	24.5 ± 6.0	39.1 ± 11.0			
Ground hunting	2	0.0	0.6 ± 0.6	1.0 ± 1.0	0.5 ± 0.4	0.455	0.231	0.754
	5	0.0	1.2 ± 1.1	1.3 ± 0.8	1.5 ± 0.8			
Flying	2	0.3 ± 0.2	7.0 ± 5.6	7.3 ± 4.2	2.5 ± 1.5	0.375	0.168	0.857
	5	0.2 ± 0.2	2.8 ± 0.7	4.3 ± 2.0	3.5 ± 1.2			
Eating self-captured prey	2	0.0	0.4 ± 0.3	2.4 ± 0.7	7.4 ± 4.1	0.061	<0.001	0.152
	5	0.0	0.1 ± 0.1	0.3 ± 0.1	3.5 ± 1.4			
Maintenance	2	17.1 ± 4.2	8.8 ± 3.3	8.2 ± 3.0	4.0 ± 2.4	0.160	0.003	0.775
	5	14.4 ± 3.8	9.0 ± 2.2	11.7 ± 2.1	7.5 ± 1.8			
Lying on belly	2	2.8 ± 2.2	7.6 ± 6.8	0.0	0.0	0.225	0.938	0.804
	5	0.2 ± 0.1	<0.1 ± <0.1	0.0	0.0			
Begging	2	1.7 ± 1.1	0.7 ± 0.7	1.1 ± 0.7	0.0	0.284	0.326	0.379
	5	3.5 ± 1.3	3.8 ± 1.7	3.2 ± 1.9	1.1 ± 0.7			
Out of sight	2	0.2 ± 0.2	3.0 ± 1.8	3.1 ± 1.5	7.6 ± 4.9	0.069	0.394	0.326
	5	3.4 ± 2.0	9.2 ± 3.1	7.5 ± 2.7	3.7 ± 1.3			
Other	2	0.6 ± 0.4	2.9 ± 1.9	0.2 ± 0.2	0.7 ± 0.7	0.628	0.889	0.326
	5	<0.1 ± <0.1	<0.1 ± <0.1	0.9 ± 0.9	1.2 ± 1.0			

[a] ANOVA for brood size, time and time × brood size across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant

[b] Total number of broods of two and five siblings observed.

behavior of American Kestrels (Varland et al. 1991). We quantified the occurrence of imitative hunting among siblings and between siblings and other kestrels. In this paper, we report the results of a test of the hypothesis that imitative social hunting in large broods increases hunting efficiency.

STUDY AREA AND METHODS

We studied a population of wild kestrels nesting in 27 nest boxes in central Iowa in 1990. A total of 24 nest boxes was attached to highway signs along Interstate Highway 35. Two nest boxes were located on farmsteads, and one was located at the College of Veterinary Medicine at Iowa State University, Ames, Iowa.

We banded all 90 young with U.S. Fish and Wildlife Service leg bands and individually marked them with colored vinyl leg jesses prior to fledging. Jesses were made with Norcross virgin vinyl (Norcross Industries Inc., West Palm Beach, FL) strips 6.5 cm long, 1.4 cm wide and riveted together, leaving a trailing tab about 3.5 cm in length.

In order to create broods of five and broods of two young, the size of broods was adjusted 1–3 d before the oldest bird in the brood fledged. Natural broods of five young were left intact and broods of <5 young were reduced to broods of two. In only two instances was it necessary to add birds to a brood; one kestrel was added to a brood of one and one was added to a brood of four. The age of these introduced young was matched closely with the age of young already in these nests. All young removed from nests, except the two introduced into broods, were released by hacking (see Barclay 1987:243) at the Iowa Department of Natural Resources Wildlife Research Station near Boone, Iowa. These adjustments resulted in 15 broods of 2 siblings each and 12 broods of 5 siblings each (Table 1).

We used backpack radiotransmitters from Holohil Systems, Ltd., Woodlawn, Ontario, Canada. Radiotransmitters were attached to one randomly selected individual in each of the 12 broods of 2; both individuals were radiotagged in three broods. Among broods of five, one individual was radiomarked in each of nine broods and five, four, and two individuals were radiomarked in each of the other three broods.

Only kestrels fitted with radiotransmitters were selected for observation as focal birds (Altmann 1974). When >1 individual in a brood was radiomarked, one fledgling was randomly selected for observation from among those visible.

Fledglings were observed between 0600–1300 H at a distance of 70–100 m with a 20× or 20–60× spotting scope. Family groups were monitored on a rotational basis; generally once during the first week after fledging and then at 1–3 d intervals until contact with all radiomarked kestrels in a brood was lost. When we could not find a radiomarked kestrel, we searched by vehicle an area of about 64 km^2 around the kestrel's last known location.

Nine radiomarked kestrels in eight small sibling groups died within 1 wk after fledging. During the first 2 wk after fledging, five radiotagged kestrels from five large sibling groups also died. Signals failed in five transmitters, two in small sibling groups and three in large, within 3 d after the radio-tagged birds fledged.

We adopted Wyllie's (1985) definition of dispersal, which is movement of a fledged bird farther than 1 km from its nest without return. We determined time of dispersal only for kestrels with transmitters known to be functioning 1 wk after fledging. Birds whose signal was lost <1 wk after fledging (N = 5) were not classified as dispersed because young kestrels at this age are relatively inactive (Varland et al. 1991). Transmitter failure was confirmed in two of these five birds when they were observed with other radiomarked siblings. Thus, it was unlikely that signal loss in the other three birds was the result of movement from the search area.

Observation sessions lasted 5 to 60 min or until the focal bird disappeared from view. We did not use data if visual contact with the bird was lost in <5 min. We attempted to initiate a second observation session with the same focal bird or with another radiomarked kestrel from the brood if the bird disappeared in 5–30 min. This resulted in a total of 15 paired sessions. For the analysis, we combined each pair of consecutive sessions into one session. We analyzed data for 85 observation sessions (mean length = 43.6 min, SD = 19.6).

A metronome timing device (Wiens et al. 1970) set at 20-sec intervals cued spot observations of behavior and social activity. At each sound of the tone, we recorded behavior and social activities of the focal kestrel. Except for the social activity subclass "social hunting," we used the classes and subclasses of activity described in Varland et al. (1991): general behavior (nine subclasses), social behavior (five subclasses), hunting behavior, and allopreening and beaking.

General Behavior. "Perch resting" describes a kestrel perched and not engaged in any other behavior. "Perch hunting" was distinguished from other perching activity by alert posture, erect body or body leaning slightly forward, frequent staring at ground, and head bobs (Toland 1987, Village 1990). "Ground hunting" was defined as a bird searching on the ground for prey for >20 sec. Searches of shorter duration involving flight from a perch were recorded as perch hunting. "Flight" was any nonhunting flight. We used the term "eating" only for kestrels eating self-captured prey. "Maintenance activity" included preening, plumage rousals (shaking), and stretching. "Lying-on-belly" describes a posture young kestrels often assumed on fenceposts, utility poles, and large tree branches "Begging" was solicitation of food from parents. "Out-of-sight" referred to a focal kestrel concealed by vegetation or other objects. A session was discontinued when a bird was out of sight >5 min. "Other" was used to categorize behaviors observed relatively infrequently: walking, hover hunting, aggressive interactions among siblings, parent-to-young prey transfers, and eating prey caught by parents. It was not uncommon for one or both adults to vocalize aggressively at observers during observation sessions (see also Varland et al. 1991). Thus, interactions between broods and parents probably occurred less frequently than they would in the absence of observers.

Social Behavior. "Association" was any activity (except social hunting) of the focal kestrel that occurred ≤3 m from one or more siblings (kestrels other than siblings were sometimes included, see Varland et al. 1991). "Nonsocial" refers to activity of the focal kestrel occurring >3 m from one or more kestrels. When we could not see whether other kestrels were ≤3 m from the focal kestrel because of dense vegetation, we recorded the kestrel's social status as "undetermined." "Social hunting" was hunting activity by the focal kestrel which occurred ≤10 m from one or more kestrels that were also hunting. This social hunting distance was increased from ≤3 m (Varland et al. 1991), because we observed that social interactions among hunting kestrels could occur at distances of up to 10 m.

Hunting Behavior. We recorded number of pounces, number of captures, and prey type. Hunting success was the percentage of pounces with known outcomes that were successful. Outcomes were unknown in 15% (46/310) of the observed pounces. In these cases, either the capture phase of prey pursuit occurred out of sight or the pursuit occurred too far away and we were unable to determine the outcome. Pounces were converted to hourly rates based on session length.

Allopreening and Beaking. We recorded the frequencies and the individuals involved in allopreening and beaking (Varland et al. 1991), forms of direct social contact.

Statistical Analyses. We grouped behavioral data by 7-d intervals starting with fledging. The experimental unit (n) was the sibling group, and the number of groups observed during each of the 4 wk that birds were under study ranged from eight to seven for sibling groups of five and from eight to three for sibling groups of two. We computed statistics for behavior, social, and hunting activity for each sibling group in each 7-d post-fledging interval for which data were available.

We used the general linear model procedure (PROC GLM, SAS Institute 1985) for an analysis of variance (ANOVA). The split-plot approach to repeated measures was used (Winer 1971) to test for differences in behavior, social, and hunting activities between large and small sibling groups of kestrels. Thus, for specific activities during the 4 wk after fledging, we conducted tests for average brood size effect, for linear trends over time, and for dif-

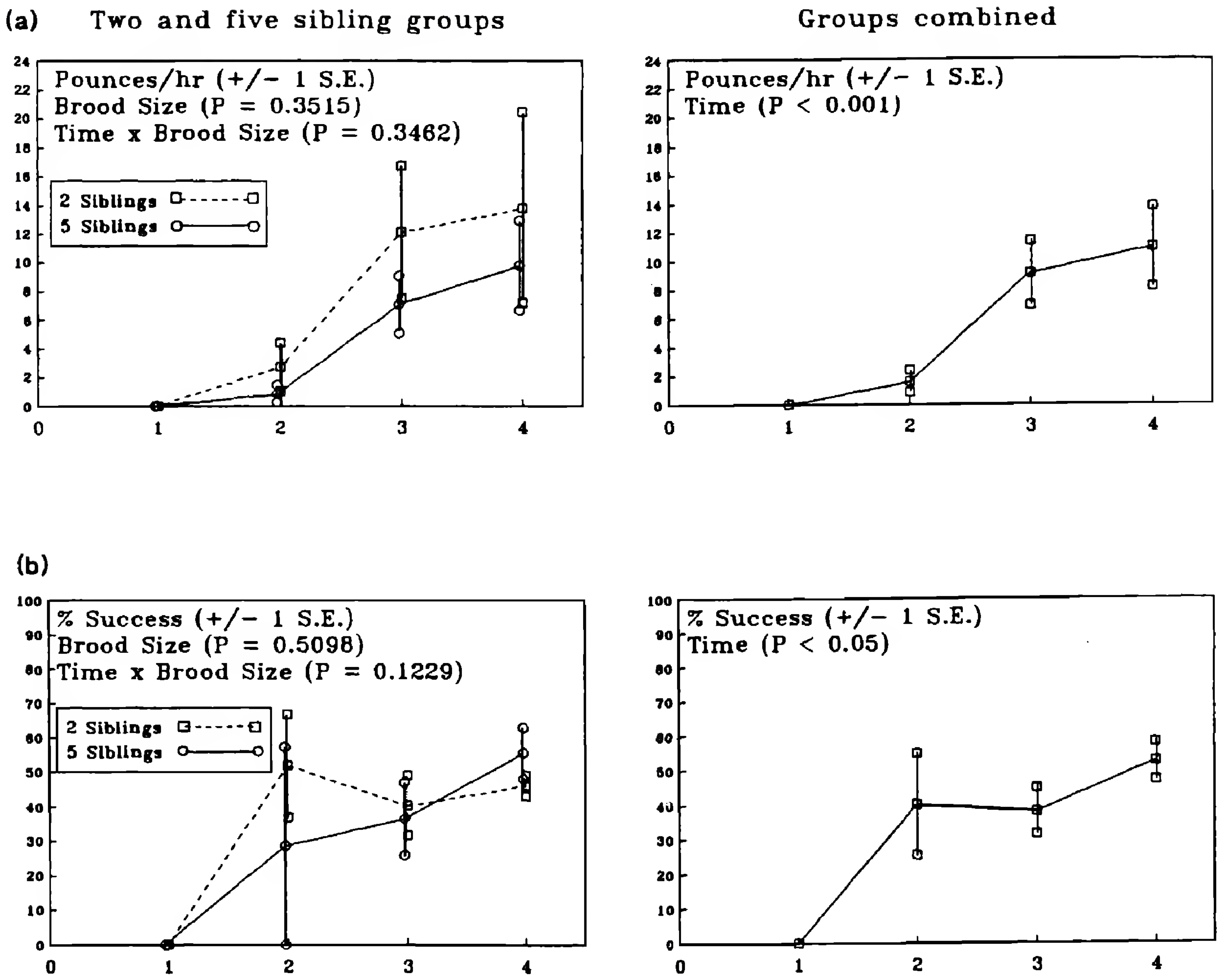

Figure 1. Mean (±SE) pounces/hr (a) and percent success (b) for sibling groups of two and five American Kestrels (left) and for groups combined (right) at weekly intervals after fledging. ANOVA for brood size, time × brood size and time effects across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant.

ferences in the rates of development (TIME × BROOD SIZE interaction). Because data were missing from some cells (not all sibling groups were represented in all weeks), we used Type III sum of squares to calculate P-values. We selected 0.05 as the level of significance for linear time trends in behavior. Because tests of several behaviors were considered in each phase of analysis, the significance level of P-values was adjusted using Bonferroni's inequalities (Snedecor and Cochran 1989:116). Thus, the level of significance for these tests is 0.05 divided by the total number of tests being made on a set of non-independent behaviors.

RESULTS

The 38 radio-marked kestrels fledged 26 May through 8 August (median = 29 June). Kestrels in a brood fledged on the same day or within 1–3 d of each other.

All tests for differences in behavior by brood size (average brood size effect) across the 4 wk post-fledging period were not significant (Table 1, BROOD SIZE). Significant decreases through time occurred in perch resting and maintenance behaviors, and significant increases occurred in perch hunting and eating self-captured prey (Table 1, TIME). The rates of decrease in perch resting and maintenance and the rates of increase in perch hunting and eating self-captured prey did not differ significantly between large and small sibling groups (Table 1, TIME × BROOD SIZE).

No differences in mean pounce rates and percent success were detected between small and large groups (Fig. 1, BROOD SIZE). Significant increases occurred with time in mean pounce rates and percent success (Fig. 1, TIME), but no differences were

Table 2. Percent time (mean percent ± SE) engaged in social and non-social activity by broods of two and five American Kestrels at weekly intervals after fledging in Iowa.

		WEEKS POST-FLEDGING				1–4 *P*-VALUES[a]		
BEHAVIOR BY SOCIAL ACTIVITY	BROOD SIZE	1 MEAN ± SE	2 MEAN ± SE	3 MEAN ± SE	4 MEAN ± SE	BROOD SIZE	TIME	TIME × BROOD SIZE
Perch resting (*N*)[b]	2	(8)	(5)	(5)	(3)			
	5	(8)	(8)	(7)	(7)			
Association	2	19.9 ± 13.6	11.8 ± 11.8	22.3 ± 13.8	0.0	0.118	0.708	0.796
	5	23.5 ± 9.5	38.1 ± 12.0	32.2 ± 8.1	23.9 ± 9.7			
Nonsocial	2	80.1 ± 13.6	88.2 ± 11.8	77.7 ± 13.8	100.0 ± 0.0	0.705	0.680	0.899
	5	71.3 ± 11.6	61.1 ± 12.2	67.4 ± 8.2	76.1 ± 9.7			
Undetermined[c]	2	0.0	0.0	0.0	0.0	0.633	0.674	0.675
	5	5.2 ± 4.1	0.7 ± 0.7	0.4 ± 0.4	0.0			
Perch hunting (*N*)	2		(1)	(5)	(3)			
	5		(2)	(7)	(7)			
Association	2	0.0	0.0	12.8 ± 12.1	13.6 ± 13.6	0.662	0.654	0.807
	5	0.0	10.1 ± 10.1	10.6 ± 11.3	9.0 ± 7.0			
Social hunting	2	0.0	8.7 ± 0.0	14.8 ± 8.4	6.2 ± 6.2	0.187	0.427	0.775
	5	0.0	38.7 ± 11.3	42.0 ± 13.4	22.7 ± 7.9			
Nonsocial	2	0.0	91.3 ± 0.0	72.4 ± 19.2	80.2 ± 19.8	0.634	0.891	0.891
	5	0.0	51.2 ± 1.2	47.1 ± 14.5	68.3 ± 13.4			
Undetermined	2	0.0	0.0	0.0	0.0	—	—	—
	5	0.0	0.0	0.3 ± 0.3	0.0			

[a] ANOVA for brood size, time and time × brood size across 4 wk post-fledging (perch resting df = 1, 28; perch hunting df = 1, 9). All tests for nonlinearity, except Perch resting/nonsocial behavior Time ($P < 0.001$), were not significant.

[b] Total number of broods of two and five siblings observed.

[c] Social status of focal bird could not be determined.

observed between small and large groups in the rates of increase of these hunting activities (Fig. 1, TIME × BROOD SIZE).

Young American Kestrels fed primarily on insects, which comprised 95% (71/75) and 97% (107/110) of the prey items caught by small and large sibling groups, respectively. At least 16% (28/178) of these insects were grasshoppers (Orthoptera). We were unable to identify the other insects caught. One bird fed on earthworms (Oligochaeta) 16 d after fledging, and three birds captured four small mammals. Two of these mammals were voles (*Microtus* sp.), and the others were not identified.

No differences in social activity were found between brood sizes (Table 2, BROOD SIZE) or in linear trends in social activity over time (Table 2, TIME). Allopreening or beaking exchanges were observed during 12% (10/85) of the observation sessions on small and large sibling groups. These two social behaviors were observed at least once in two of the small broods and in six of the large broods.

Social hunting occurred during 51% (21/41) of the sessions in which hunting was observed in small and large broods. Social hunting was observed at least once in 50% (4/8) of the small broods and in 75% (6/8) of the large broods. For sessions in which social hunting was observed ($N = 21$), 72% involved siblings only, 14% involved siblings and parents, and 14% involved siblings and unrelated kestrels.

Mean time of dispersal was 23.2 d for small broods ($N = 6$, $SE = 1.9$) and 26.7 d for large broods ($N = 7$, $SE = 2.0$). This difference was not significant (ANOVA, $P = 0.299$).

DISCUSSION

All tests for average brood size effects for kestrel behavior, hunting, and social activities were not significant. When trends in behavioral change over time were detected, no significant differences occurred in the rates of change between small and large broods. Thus, broods of two and five kestrels did not differ in behavior, social, or hunting activity during the 4 wk that broods were observed.

Although we were unable to demonstrate any brood size effects, the power of our statistical tests was low because of small sample sizes. Small sample sizes increase the probability of Type II error (Snedecor and Cochran 1989).

Mortality or loss of the radio signal was high among radiotagged kestrels the first week after fledging, and resulted in 47% (15 to 8) and 33% (12 to 8) decreases in sample sizes for groups of two and five siblings, respectively. This high mortality was unexpected. Only 2 of 26 birds radiomarked in 1988 and 1989 died (Varland 1991). Predation was the largest source of mortality for small and large broods, and accounted for 9 of 14 deaths.

Kestrels wearing radiotransmitters may have been vulnerable to predation. The mean weight of transmitters in this study was 6.2 g, which is 5% of the mean weight of adult male American Kestrels (112 g) and is 4% of the mean weight of adult females (141 g; Cade 1982). These percentages are within the 3–5% of body weight limits recommended for transmitters used on birds (Hegdal and Colvin 1986). While we observed no obvious behavioral differences between fledglings wearing transmitters and those that were not wearing them, the study was not designed to make a quantitative comparison between marked and unmarked groups.

Starvation was not an important cause of mortality (1 of 14 deaths), but may have been significant later in the first year of life. Because of movement of young away from their natal areas, we were unable to observe any kestrel longer than 39 d after fledging. Starvation was the most important cause of mortality after independence from their parents among juvenile Yellow-eyed Juncos (*Junco phaeonotus*; Sullivan 1989) and Tawny Owls (*Strix aluco*; Hirons et al. 1979).

Young kestrels presumably learn hunting skills during the first 4–6 wk after fledging. Imitative social hunting during this period may provide an adaptive advantage to individuals later in the juvenile period, if there is sufficient selection for learned efficiency in hunting. Mean hunting success from perches in this study and in earlier research (Varland et al. 1991) did not exceed 55%. This is a substantially lower success rate than previously reported for older kestrels hunting invertebrates (Collopy 1973, Smallwood 1987, Toland 1987).

This study has left open to question whether imitative social hunting by American Kestrels after fledging influences hunting efficiency. If learning does occur during the development of hunting, perhaps siblings learn more from observing their parents than they learn from each other. Our study was not designed to test this idea. Further research is needed to document whether social hunting influences hunting efficiency in American Kestrels.

ACKNOWLEDGMENTS

This paper is a contribution of the Iowa Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service; Iowa State University; Iowa Department of Natural Resources; and the Wildlife Management Institute It is Journal Paper No. J-14767 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 2845. Support was received from the Iowa Department of Transportation, Iowa Department of Natural Resources Nongame Program, Iowa Ornithologists' Union, North American Bluebird Society, Iowa Science Foundation, Big Bluestem Audubon Society of Ames, Iowa, Max McGraw Wildlife Foundation, Iowa Agriculture and Home Economics Experiment Station, and the Iowa State University Department of Animal Ecology. We are grateful to ISU students T. Holmes, B. Warson, and J Humble for assistance in the field and to DNR Nongame Technicians B. Ehresman and P. Schlarbaum for managing the kestrel hacking station. We appreciate the assistance of E. Klaas, L. Best, J. Dinsmore, and K. Shaw, who helped us formulate this concept-based study. Reviewers whose help was appreciated were: E. Klaas, L. Best, J. Dinsmore, K. Shaw, L. Igl, J. Smallwood, S. Sherrod, and G. Bortolotti.

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Received 24 December 1991; accepted 28 March 1992